Infanticide

Comparative and Evolutionary Perspectives

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INTRODUCTION

There are inherent difficulties in reviewing the sources of mortality in wild carnivores. Besides the fact that mortality has often been inflicted by fieldworkers themselves, most carnivores are nocturnal, solitary, and wary of human observers. Consequently, ecological studies often consist solely of analyses of feces, and ranging studies are often based on the movement patterns of radio collars worn by unseen animals. Furthermore, even intensive direct observations do not always provide good data on cub mortality because female carnivores keep their young hidden for the first few weeks or months of life. Most cub mortality, therefore, must be inferred from disappearance, and the causes of death remain unknown. Finally, attributing death to infanticide presents special difficulties in carnivores. An observation of a carnivore eating a conspecific is not conclusive evidence of intraspecific predation: carnivores are usually scavengers as well as predators.

However, because of their carnivorous habits and because most bear altricial young, carnivores are more likely to exhibit infanticide than any other mammalian order. Infanticide can occur in several contexts, and examples of the phenomenon are discussed according to the identity of the perpetrator:

1. Infanticide by males
2. Extragroup infanticide

3. Intragroup infanticide by females
4. Intralitter infanticide

Infants are defined as immatures dependent on their mothers and *infanticide* as any behavior that directly induces infant mortality. Thus, as well as the infliction of mortal wounds on infants, infanticide includes harassment of the mother until she can no longer care for her young and apparently deliberate abandonment of young. Cases of infanticide in captivity that appear to be the consequence of an artificial environment are excluded (e.g., during group formation: Rabb *et al.*, 1967; or during an experiment in extreme crowding: Rasa, 1979). Inferences drawn from observations on captive animals are explicitly noted.

INCIDENCE OF INFANTICIDE IN CARNIVORES

Infanticide by Males

Lions. The most extensive data on infanticide by males come from the studies of the African lion (*Panthera leo*) in the Serengeti and Ngorongoro Crater, Tanzania. Between 1966 and 1973, four cases were found of newly arrived males killing one or more cubs in prides that they had just taken over (Bertram, 1975a). Published details are available for only one of these cases. Two males resident in the Kamarishe pride entered the Seronera pride's range and killed three small cubs while their mother was elsewhere (Schaller, 1972). The two Kamarishe males then evicted the resident male of the Seronera pride and later returned to the corpses of the dead cubs. One male ate the viscera of one of the cubs. The Kamarishe pride then shifted its range for 5 months, and the Kamarishe males were not seen mating with females of the Seronera pride until 6 months after killing the cubs.

In 1980, we made a fifth observation of infanticide by male lions. We heard sounds of a fight, and arrived to find a male eating what appeared to be the remains of a small cub. The male then approached the mother, she snarled at him, and he plunged his head into the grass beside her. The mother and a second female both attacked him. When the male withdrew, the mother picked up from the same spot in the grass a dead, 2-month-old cub, still bleeding from bite wounds. A third cub, seen escaping into the bushes during the fight, disappeared within 2 weeks. The infanticidal male was one of a group of four males that were simultaneously resident in two adjacent prides. His three companions started to associate with this third pride 6 months before the infanticide, but the infanticidal male was not seen with the pride until 6 weeks after the mother had conceived and was not observed with the female again until the day he killed the cubs. During the period in which the mother had conceived, a second male group was also

observed mating with these females. Several weeks after killing her cubs, the infanticidal male was observed consorting with the female.

Finally, in July 1982, S. J. Cairns (personal communication) observed a nomadic male kill a small cub that was following 100 m behind two females and two other cubs. The females were not the mothers of any of the cubs and retreated from the male. The male had taken the cub's body into thick vegetation in the morning and was again seen carrying a dead cub that night. It is not known whether he was still carrying the corpse of the first cub or had killed a second cub because none of these cubs was seen again. The male had not associated with the pride before, and there is evidence that a male take-over was in progress.

In a separate study at the northern end of the Serengeti ecosystem, Jackman and Scott (1982) observed one of three newly arrived males kill two small cubs. The new males became resident in the pride, and the infanticidal male might have fathered the female's next litter.

In addition to these seven observations, there is circumstantial evidence that infanticide occurs almost every time a new coalition of males takes over a pride. A *male take-over* is defined as the complete replacement of one coalition of males by another. Bertram (1975a) showed a significant increase in mortality of cubs less than 2 years old in the first 4 months after a take-over. In our study, there was a significant increase in the mortality of cubs whose fathers were replaced by a new coalition of males before the cubs were 4 months old (Table I), and all the older cubs (belonging to seven females) were evicted within 3.5 months of the take-over (Packer and Pusey, 1983a,b). Small cubs almost always disappeared within the first 2 months after

Table I. Mortality of lion cubs[a]

	Fathers replaced in first 4 months (%)[b]	Fathers remain in pride for first 6 months (%)[c]
All cubs in litter die before 6 months of age	89.5	40.8
At least one cub in litter survives to 6 months of age	10.5	59.2

[a] Mortality of lion cubs when their fathers were replaced by a new coalition of males (based on 10 take-overs) is contrasted with mortality of cubs when their fathers remained in the pride. Because cubs are unable to survive on their own until at least 18 months of age (Bertram, 1975a), mortality also includes cubs that disappeared. Chi-square = 13.20, $p < 0.001$.

[b] $N = 19$ litters.

[c] $N = 98$ litters.

a take-over. The only take-over in which small cubs survived involved "new" males returning to their natal pride. One of the two females whose cubs survived was a full sibling of all three incoming males. In all other cases, the incoming males were not close relatives of the infants and had not been seen associating with the females before.

We also had evidence of infanticide during an attempted take-over. An alien group of males was seen well within the pride range of a group of two lactating females with six cubs. On the same day, one female and two cubs disappeared, and the surviving female was wounded. The missing cubs were 4 months old and were the offspring of the surviving female, so the disappearances do not indicate a splitting up of the pride. In another case, we observed a male coalition chase away the resident males of a neighboring pride, then return to where the three females were keeping their cubs. The mothers attacked the intruding males, all three females were wounded, but no cubs were lost, and the intruders returned to their own pride. Two years later, yet another male group intruded into the range of the same three females. Coincident with this intrusion, one lactating female disappeared, and the others were wounded (though again no cubs were lost). We, therefore, assume that the missing mothers in this and the first case died while defending their cubs.

Although there are a number of direct observations of males killing infants in these studies, many more cases are inferred from the coincident disappearance of cubs at the take-over. It is also possible, as Bertram (1975a) pointed out, that females sometimes abandon their cubs at a take-over or are kept from their cubs by the new males until the cubs die of stravation; but this is difficult to determine. From our observations of attempted take-overs, we suspect that females more often defend their cubs than abandon them. Bertram (1975a) also suggested that females might abort upon exposure to new males. However, we found a number of cases where pregnant females did not abort at a take-over (Table I includes nine females that were pregnant at a take-over and gave birth to live young) (see Packer and Pusey, 1983a,b).

In summary, infanticide appears to be a regular feature of male take-overs in lions in Northern Tanzania and as such appears to be a reproductive strategy by males (Hrdy, 1974; Bertram, 1975a). Females with surviving offspring remain anestrus until their cubs are about 1½ years old but resume mating activity within days or weeks of losing their cubs (lions in East Africa do not breed seasonally) (Schaller, 1972; Bertram, 1975a; Packer and Pusey, 1983a). Since the infanticidal males nearly always remain with the pride after the take-over, the females mate with the infanticidal males.

Females that lose small cubs at a take-over conceive again an aver-

age of 134 days after the loss, whereas females whose cubs survive show an average postpartum amenorrhea of 530 days and then conceive about 1 month later (Packer and Pusey, 1983a). Because there is considerable cub mortality even in the absence of male take-overs (Bertram, 1975a; and Table I), it is probably more appropriate to include females whose dependent cubs died under other circumstances than a take-over with females whose cubs survived to independence. Over all these females, average postpartum amenorrhea is 345 days, and conception occurs about 1 month later (Packer and Pusey, 1983a). Thus, by killing small cubs when they first take over a pride, males sire cubs about 8 months sooner on average than they would if they allowed the cubs of the previous males to survive. The average tenure length of males is only 2 years (Bygott *et al.,* 1979) and males might sometimes fail to breed if they did not speed up the return to receptivity of the females of their new pride. Furthermore, cub mortality is higher if there are older cubs present in the pride, and by removing the cubs of the previous males, incoming males enhance the survival of their own cubs (Bertram, 1975a).

In other parts of East Africa, there is only anecdotal evidence of infanticide by incoming males (Adamson, 1968; Cullen, 1969). However, male take-overs occur at a much lower frequency in the smaller parks because they contain only small isolated lion populations, and migrating males suffer high mortality outside protected areas (Van Orsdol, 1981).

Other species. In all other carnivore species, evidence of infanticide by males is largely anecdotal. Besides listing examples of infanticide, information is also included on the relevant reproductive parameters of females that determine whether or not males would gain a reproductive advantage from killing young.

Schaller (1967) cited two cases reported by hunters of male tigers (*Panthera tigris*) apparently killing cubs. There are also a number of suspected cases of infanticide from a detailed study of tigers (J. L. D. Smith, in preparation). Tigers are solitary, and the range of each territorial male overlaps those of several females (Sunquist, 1981). A territorial male died whose range included seven females. Three 6- to 13-month-old male cubs belonging to three females were found dead shortly after new males had replaced the territorial male (Smith, in preparation). In three other cases, litters disappeared coincident with male replacements. The new males could not have been the fathers of the cubs, and several were subsequently resident in the area long enough to have fathered the females' next litters. Tigers are not seasonal breeders, and the interbirth interval is about 2 years (Sankhala, 1967). Thus, a male would probably father cubs more quickly if he were to kill the small cubs in his new territory.

In pumas (*Puma concolor*), there are three reports of males killing

cubs. The only details available on the first are that two cubs of a single litter were killed (Hornocker, 1970). In the second, on two occasions a hunter found cubs that had been "apparently killed by mature males" but were uneaten (Robinette et al., 1961). In the third, a male killed and ate the cubs of a female that had been shot by a hunter (Young, 1927). In the last case, the infanticidal male was assumed by the author to have been the father of the cubs, because after the shooting his range included the site of the shot female's den. However, there was no information on associations between the male and the female prior to the shooting.

Pumas tend to breed seasonally (Robinette et al., 1961; Hemker, 1982), and the interbirth interval is usually about 2 years (Robinette et al., 1961; Hornocker, 1970). The loss of small cubs is likely, therefore, to cause the females to resume breeding 1 year earlier than if their cubs survived. However, there are no data on the subsequent reproductive activity of infanticidal males in pumas or is it known if the infanticidal males were unrelated to the cubs they killed.

In cheetah (Acinonyx jubatus), infanticide by males appears to be rare, although there is one case in Masai Mara, Kenya where a male was suspected of killing a female's 1-week-old cubs (Burney, 1980). In 1978, a male was seen fighting with a mother of newborn cubs near where the cubs were hidden. The male appeared to be searching for the cubs, but the cubs survived the incident. In 1979, a second male was seen fighting with the same female near the lair of a new set of cubs on the day that two of the cubs disappeared. Since the male had previously associated with the female, he might have been the father of the second litter (D. and L. Burney: personal communication).

In the adjacent Serengeti, females with cubs of several months of age have been seen to be "pinned down" temporarily by coalitions of males that are probably not related to the cubs, but little overt aggression is directed at the cubs, and the behavior of the males is not believed to cause cub mortality (T. M. Caro, personal communication). No infanticide has been observed in nearly 6 years of intensive study of cheetah in the Serengeti (G. W. Frame and T. M. Caro, personal communication).

In the Serengeti, cheetah do not breed seasonally and have an interbirth interval of about 18 months (Frame, 1980; G. W. Frame, personal communication). The ranges of females are much larger than those of males (Frame, 1980), and thus females must frequently encounter males that are not the father of their cubs. Because the loss of small cubs would speed up the reproduction of females, the apparent rarity of infanticide by male cheetah is an anomaly.

Infanticide by males is believed to be common in brown bears (Ursus arctos). Troyer and Hensel (1962) reported two cases of male brown

bears killing and eating cubs and a third case of a male having eaten a cub. They suggested that males frequently kill small cubs during the mating season. Perry (1966) reported two cases in polar bears (*Ursus maritimus*) where males killed but did not eat cubs. However, in both cases the cubs' mothers had recently been shot by hunters. The cubs were killed only a short time after their mothers' deaths by males that had not been present at the shootings. Jonkel (1970) reported one case where a male was found eating a freshly killed female and her two cubs. He inferred from signs of fighting that the male had killed them. Because females and cubs can run much faster than males, Stirling (1974) stated that it is "unlikely that intraspecific predation occurs at more than an incidental level" in polar bears. But Stirling also reported that "cubs were extremely nervous in meetings with any unrelated bear."

Both species of bears breed seasonally but have a 2-year interbirth interval (Ewer, 1973), thus infanticide would have a similar effect on the reproduction of females as in pumas. However, as in pumas nothing is known of the relationships between the infanticidal males and the females and her cubs.

Russell (1981) observed one case of infanticide by an alien male in coatis (*Nasua narica*) and presented evidence that such killings are common, and that they were made by males that were not close relatives of the infants. However, infanticide does not appear to be a male reproductive strategy in this species. Since coatis only breed seasonally and females apparently breed each year, infanticide does not speed up the reproduction of the females. Also, the infanticidal male does not remain to breed with the females. Russell suggested that males utilize conspecific young as prey during times of food shortage (also see Sherman, 1981).

Although we know of no other carnivore species where infanticide by incoming males has been recorded, there are few other studies where immigration of males has been observed. In dwarf mongooses (*Helogale parvula*), breeding is seasonal and annual, and most takeovers by males occur at the mating season when the preceding year's young are no longer so vulnerable to predation (J. P. Rood: personal communication).

Although infanticide by males has not been observed in spotted hyenas (*Crocuta crocuta*), Kruuk (1972) made several comments that merit attention. A spotted hyena den is largely excavated and maintained by the cubs, with the result that they are inaccessible to adults. Kruuk attributed both this and the fact that females are larger than males to the danger that males pose to cubs. Females are dominant to males as a result of their greater size, and the nature of the den results in the cubs being protected from males during their mothers'

absence. Little is known of the social dynamics of a clan, but males do often move into the ranges of other clans (Kruuk, 1972; van Lawick and van Lawick-Goodall, 1971) and are therefore likely to contact dens where they are unrelated to the cubs. Because female spotted hyenas show a long interbirth interval and do not breed seasonally (Kruuk, 1972), infanticide would be likely to cause them to resume breeding more quickly.

Extragroup Infanticide

There are several examples of individuals of one breeding group killing the young of another group. Camenzind (1978) had evidence of two cases where invading packs of coyotes (*Canis latrans*) killed the pups of neighboring packs. P. Moehlman (personal communication) came upon an invading family of golden jackals (*Canis aureus*) feeding on the pups of the resident family. However, the jackal pups might have died of other causes prior to being found by the invading pair. Frame and Frame (1981) observed an invading pack of wild dogs (*Lycaon pictus*) chase and scatter a resident pack, and one 15-week-old pup of the resident pack was never seen again. However, the missing pup might have disappeared because it was unable to relocate the rest of its family.

Schaller (1972) observed a nomadic female lion stalking the 7- month-old cub of another female, and the next morning the nomad was found eating the freshly killed cub. Schaller also saw a female kill two small cubs of another pride. J. D. Bygott and J. P. Hanby (personal communication) made two similar observations. First, a female from one pride entered the hiding place of the small cubs of an adjacent pride, and the cubs were never seen again. Second, one 9-month-old cub and one 15-month-old cub were killed in an interpride encounter that apparently involved no males.

In many of these cases, the young died when their parents were not in the immediate vicinity. Camenzind (1978) saw coyote packs successfully defend dens against invaders on five occasions.

Intragroup Infanticide by Females

Infanticide by the mother. In a few species, there are observations of deliberate abandonment of healthy young by their mothers (see Carlisle, 1982, for review). In lions, there is a striking tendency for females to abandon their litters when only one cub remains. Rudnai (1973) reported three cases of wild females abandoning healthy, single surviving cubs of less than 3 months of age, three cases by George Adamson's free-ranging females, and five cases by captive females. In the Serengeti, we twice observed mothers abandoning their single cubs of only a few weeks of age. Each mother carried her cub into an open area. In

both cases, the cub was too small to move to cover and disappeared on the same day. Both cubs appeared to be in excellent health and both were males. Tait (1980) cited two cases of female grizzly bears (*Ursus horribilis arctos*) abandoning single cubs. Average litter size in lions and grizzly bears is between two and three, and both Rudnai and Tait calculated that females in these species would increase their lifetime reproductive success by abandoning single cubs and investing exclusively in larger litters.

Schaller (1972) observed a female lion abandon one of three healthy cubs but believed that she had not done so intentionally. We observed a female lion abandon two of her three starving cubs during a period of extreme prey scarcity: the mother and two of her pridemates were leading their cubs to a new location, and when her two weakest offspring fell behind, she called to them but did not return for them.

Infanticide by females other than the mother. A common feature of carnivore social structure is the presence of only one breeding female within a group. This is typical of canids (Kleiman and Eisenberg, 1973) and is also found in dwarf mongooses (Rood, 1980) and European badgers (*Meles meles*) (Kruuk, 1978).

In species where there is only one breeding female but more than one adult female present in the group, there is sometimes evidence of infanticide by the breeding female of the offspring of subordinate females. The dominant female was observed to kill a subordinate female's pups in wild dogs (van Lawick, 1974) and was suspected of having done so in captive wolves (*Canis lupus*) (Altmann, 1974). In captive red foxes (*Vulpes vulpes*), harassment of a subordinate female by the dominant female resulted in the death of the subordinate's cubs (Macdonald, 1979). In wild dogs, there are other examples of subordinate females giving birth, but the pups almost never survive (Frame *et al.*, 1979). In dwarf mongooses, subordinate females regularly mate but fail to become pregnant, and if they do conceive, their litters regularly disappear (Rood, 1980). Although there is no direct evidence of infanticide, Rood suggested that the cubs might be killed by the dominant female.

Brown hyenas (*Hyaena brunnea*) show an interesting parallel to these species. Clans of brown hyenas contain more than one breeding female and share communal dens (Owens and Owens, 1979), but the births within the group are so widely spaced that only one female in the clan has small cubs at a time (D. D. Owens: personal communication; also see Mills, 1978). In the only observation of two females giving birth synchronously, the dominant of the two females harassed the subordinate to an unusual extent, and within a few days the subordinate had lost her cubs (D. D. Owens, in preparation).

An important consequence of the behavior of the dominant female

in all these cases is that the subordinate female ended up helping to rear and (except in the wolves) even to suckle the offspring of the dominant female. It is likely that this form of infanticide represents an adaptive strategy by the dominant female: the infanticidal female both enforces her position as the only breeding female within the group and also ensures that her offspring receive additional care (also see Emlen, 1982; Macdonald and Moehlman, 1982). If the subordinate female were able to breed, her offspring would be in competition with the young of the dominant female, and the subordinate female would be expected to care for her own young rather than act as a helper for the dominant female. In all cases except the brown hyenas (where kinship was unknown), the "exploited" subordinate female was a close relative of the breeding female and, consequently, so were the victims of the infanticide.

There is one possible case of a female helper killing her younger siblings in golden jackals (van Lawick and van Lawick-Goodall, 1971). A young female was found eating a small pup at her mother's den, but the pups had been in poor health on the previous day. Although they mention that the helper might have killed it, the authors suspected that the pup had already died before the helper had found it. Detailed studies of the effects of helpers on pup survival in silverback jackals (*Canis mesomelas*) (Moehlman, 1979) and golden jackals (Moehlman, 1982) suggest that helpers usually increase pup survival rather than act as a source of mortality.

Intralitter Infanticide

Although siblicide is a common phenomenon in newly hatched birds (see Mock, Chapter 1, this volume), evidence in carnivores is extremely difficult to collect because most cubs are kept in dens and most observers are unwilling to destroy or disturb a den in order to observe them. However, Macpherson (1969) found a den of arctic foxes (*Alopex lagopus*) in which six of nine pups had been killed by a bite at the base of the skull. After taking two of the survivors into captivity, one killed the other in a fight over food, inflicting a wound similar to those found in the six dead pups at the den. Macpherson suggested that siblings often kill each other during times of food shortage.

Relevant to this section is a bizarre case in spotted hyenas in which two three-quarters-grown cubs were each found strangling 2-month-old cubs during the excavation of a den by Watson (1965). The two sets of cubs had been sharing the den and entered it on this occasion to avoid the scientists. The killings were presumably elicited by the panic of the young in response to the disturbance of the excavation: young spotted hyenas commonly survive the experience of sharing a den with older cubs (Kruuk, 1972).

DISCUSSION

It is almost impossible to estimate accurately how commonly infanticide occurs in carnivores. Evidence in most species is only anecdotal but, as pointed out at the beginning of this chapter, it is extremely difficult to collect good data on most species of carnivores. It is worth stressing that causes of cub mortality in carnivores almost always have to be inferred. For example, Schaller (1972) estimated that the most frequent cause of death in lion cubs was starvation, and although he provided compelling evidence in support of this, he did not mention ever having observed the moment of death in a starving cub. We have also seen many cubs that were obviously starving but have observed the death of only one starving cub.

Most carnivores will eat almost any small mammal that they can easily capture and kill, including a conspecific. In several species, adults have even been known to kill and eat large subadult and adult conspecifics (e.g., pumas: Lesowski, 1963; lynx (*Lynx canadensis*): Elsey, 1954; polar bears: Jonkel, 1970; and hyenas: Kruuk, 1972).

Because of the difficulties, therefore, in determining whether a specific case of infanticide constitutes an example of "spite," intraspecific competition, or simply of predation, we are reluctant to discuss all possible ways in which infanticide may be of adaptive significance in carnivores (instead, see Hrdy, 1979; Sherman, 1981). Here we concentrate on the following adaptive interpretations:

1. Infanticide is a female reproductive strategy by which a dominant female ensures that she is the only female in the group to breed at that time and also that her offspring receive care from the subordinate female. Furthermore, the dominant female's offspring are consequently not subject to competition for resources from the offspring of the subordinate (Hrdy, 1979). There are only a few examples of this behavior in any one species, but evidence comes from several species: wild dogs, red foxes, wolves, dwarf mongooses, and brown hyenas.

2. Infanticide is a reproductive strategy whereby males terminate the female's investment in the offspring of other males and stimulate a rapid resumption of receptivity (Hrdy, 1974; Bertram, 1975a). Although there are numerous examples of males killing infants, the existence of infanticide as a male reproductive strategy can only be confirmed in lions and possibly in tigers.

Most carnivores are solitary (Ewer, 1973), and even most "social" carnivores live in groups composed of only one breeding female. Only a few species (lions, some mongooses, and spotted hyenas) typically form social groups where more than one female breeds simultaneously.

Female carnivores, therefore, may be viewed as typically intolerant of the proximity of other breeding females. However, the existence of even a few species that form groups containing multiple breeding females and the more common existence of groups containing non-breeding female "helpers" as well as the single breeding female suggest that shifts in ecological variables (Macdonald, 1979; Waser, 1981) or hunting styles (Kleiman and Eisenberg, 1973; Kruuk, 1975) can lead to a change in social structure.

Therefore, there are likely to be conditions that result in conflict between females of the same group over whether the subordinate female also breeds or only helps rear the young of the dominant female, and infanticide by dominant females may be a manifestation of such conflict. (Note that the females are usually close relatives in these cases.) Ordinarily, the reproduction of the subordinate is suppressed by the behavior of the dominant (e.g., wolves: Zimen, 1976; red foxes: Macdonald, 1978; and dwarf mongooses: Rood, 1980), and infanticide in these species is an extension of this suppression (see Kleiman, 1980; McClintock, 1983).

The wide dispersion of females, together with strict seasonal and annual breeding, probably prevent infanticide as a male reproductive strategy from being ubiquitous in carnivores. Most monogamous species appear to be bonded for life, so that male tenure length is typically long, and male–male competition is not so severe as it is in highly polygynous species. Males in these species invest their reproductive effort in helping to rear offspring rather than in maximizing their number of mating partners (Trivers, 1972).

Because of the enormous difficulties of studying nocturnal and solitary species, relevant data on them are not available in proportion to the frequency of this type of social organization across species of carnivores. Like tigers, most solitary species are polygynous: males have territories that overlap those of several females (Ewer, 1973). Thus, infanticide as a male reproductive strategy may be confirmed eventually in many solitary carnivore species where the female's reproduction is accelerated by the death of her young.